Orientation perception anisotropies indicate functional segregation within the color system

Ilias Rentzeperis
Institute of Neuroinformatics, University of Zurich and Swiss Federal Institute of Technology, Zurich, Switzerland
Brain & Cognition Research Unit, University of Leuven, Leuven, Belgium
RIKEN Brain Science Institute, Wako-shi, Japan

David M. Alexander
Brain & Cognition Research Unit, University of Leuven, Leuven, Belgium

Daniel C. Kiper*
Institute of Neuroinformatics, University of Zurich and Swiss Federal Institute of Technology, Zurich, Switzerland

Cees van Leeuwen*
Brain & Cognition Research Unit, University of Leuven, Leuven, Belgium
Kaiserlautern University of Technology, Kaiserslautern, Germany

When stimuli are luminance-defined, the visual system is known to prefer those that are radially oriented with respect to the point of fixation over tangentially oriented ones (the radial bias effect). In two contrast detection experiments and an orientation discrimination experiment, we investigated whether the radial bias effect also exists for chromatic stimuli. The contrast detection experiments revealed the radial bias effect to be color-specific; the effect was present for isoluminant red-green stimuli but absent or in the opposite direction for blue-yellow stimuli with, respectively, low (0.4 c/°) and medium (1 c/°) spatial frequencies. In agreement with previous results, we also found distinct sensitivity distributions for red-green and blue-yellow signals as a function of eccentricity. The results, thus, demonstrate a functional segregation between red-green and blue-yellow signals not only in local but also in nonlocal signal processing.

Introduction

Anisotropies provide insight into the way the visual system analyzes information. For instance, a variety of experiments have shown that humans are more sensitive to stimuli oriented horizontally or vertically than obliquely (Berkley, Kitterle, & Watkins, 1975; Campbell & Kulikowski, 1966; but also see Essock, DeFord, Hansen, & Sinai, 2003 and Wilson, Loffler, Wilkinson, & Thistlethwaite, 2001 for the opposite effect). This effect, called the oblique effect (Appelle, 1972), indicates that our visual system is locally tuned to the cardinal orientations.

Not all orientation anisotropies, however, are local. Observers are more sensitive to eccentric stimuli that are oriented towards the fovea (radial orientations) than to ones oriented perpendicularly (tangential orientations) (Bennett & Banks, 1991; Berardi & Fiorentini, 1991; Fahle, 1986; McGraw & Whitaker, 1999; Rovamo, Virsu, Laurinen, & Hyvarinen, 1982; Sasaki et al., 2006; Scobey & van Kan, 1991; Temme, Malcus, & Noell, 1985; Westheimer, 2003, 2005). This effect is known as the *radial bias* effect.

We refer to *nonlocal* processes as the ones that can be modulated or even driven by a signal or an interaction of signals that are not constrained within a local region in the visual space. The *radial bias* effect is an example of *nonlocal* orientation tuning within the visual system since the relevant property is orientation of the stimulus in the periphery relative to the fixation location. Typically, *nonlocal* processes are modulating their responses based on contextual information such as

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grouping cues. The underlying mechanisms of *nonlocal* processes may be distinct from the local ones.

The *radial bias* effect has predominantly been studied with luminance-defined stimuli; here we investigate whether it also occurs for stimuli defined exclusively by chromatic contrast. Having distinct orientation sensitivity profiles between chromatic and luminance signals would imply that *nonlocal* orientation is processed in a color-specific manner. Such color-specificity would suggest functional segregation between color and luminance channels in *nonlocal* orientation processing. Likewise, if we obtain distinct *nonlocal* orientation sensitivity profiles between different colors, this result would suggest functional segregation amongst the color channels.

We performed three experiments: two variations of a contrast detection task and one orientation discrimination task. In these experiments, we examined the *radial bias* effect for achromatic and chromatic signals, using luminance and isoluminant red-green (R/G), blue-yellow (B/Y) Gabor patches, presented at different eccentricities. In the first contrast detection experiment we used spatial frequencies that were optimized for contrast sensitivity. For colored Gabors maximum contrast sensitivity was exhibited for a low spatial frequency, 0.4 c/°; for luminance Gabors the optimal spatial frequency was greater, 1 c/°. We found for these stimuli that contrast detection thresholds for radially oriented Gabors were lower compared to tangentially oriented ones for R/G and luminance patterns. This effect was not observed for B/Y patterns. In the second contrast detection experiment we used chromatic and luminance Gabors at the same spatial frequency (1 c/°). By doing so we probed color responsive mechanisms that are jointly selective to a spatial scale useful for form processing. The difference in sensitivities between R/G and B/Y in this case was even stronger: Participants showed greater sensitivity to radial orientations compared to tangential ones for R/G stimuli; the reverse was true for B/Y stimuli. The result of the contrast detection experiments suggests that with respect to *nonlocal* anisotropies, luminance and R/G mechanisms are different from B/Y ones. Furthermore, the rate of increase in contrast detection thresholds with respect to eccentricity was distinct for low spatial frequency R/G and B/Y patterns, with R/G patterns having a steeper increase than B/Y ones.

In a third experiment we studied *radial bias* effects in orientation discrimination thresholds. Previous studies have investigated orientation discrimination thresholds for color and luminance patterns presented at the fovea (Beaudot & Mullen, 2005; Reisbeck & Gegenfurtner, 1998; Webster, De Valois, & Switkes, 1990; Wuerger & Morgan, 1999). Stimulus contrast was defined in equal multiples of contrast detection thresholds. We did not find a *radial bias* effect in orientation discrimination with color patterns or any difference in orientation discrimination sensitivity profiles between R/G and B/Y patterns.

Methods

Participants

Seven participants (median age 31; five males, two females), including two of the authors, took part in Experiment 1. Four of them (median age 28; five males, two females) subsequently also took part in Experiment 3. With the exception of one of the authors, all these participants were Masters or PhD students in the Institute of Neuroinformatics in the Swiss Federal Institute of Technology (ETH). Four participants (median age 32, all males), including two of the authors, took part in Experiment 2; one of the authors participated in all three experiments. In total ten different individuals took part. All were experienced psychophysical observers with normal or corrected–to-normal vision and gave their informed consent prior to participating in the experiments.

Stimuli

The stimuli were luminance and chromatic Gabor patches defined by their position in the physiologically based DKL color space (Derrington, Krauskopf, & Lennie, 1984). DKL color space consists of three axes: two of them where chromaticity changes and luminance remains fixed and a third one where chromaticity remains fixed and luminance changes. Along one of the color axes (R/G axis) the signal from short-wavelength (S) sensitive cones remains fixed and the signals from long- (L) and middle-wavelength (M) sensitive cones covary so that their sum remains fixed. Along the other color axis (B/Y axis), only the signal from short-wavelength (S) sensitive cones changes. Along the luminance axis all three signals vary proportionally. The isoluminant plane is on the plane of the color axes where luminance is zero. A point in the DKL color space is defined by three parameters: the azimuth, which is the angle of the projection of the point on the isoluminant plane with the R/G axis; the elevation, which is the angle of the point and its projection on the isoluminant plane; and the amplitude, which is the length of the point from the intersection of the axes.

Gabor patches are defined as the product of a sinusoid and a Gaussian distribution. We used a circular Gaussian (both cardinal directions had the

same variance). Three types of Gabor patches were used: luminance, R/G, and B/Y. The three different types were defined by vectors aligned along the three cardinal directions in the DKL space. The contrast of the Gabors was represented by the magnitude of the vectors, their chromaticity by the direction of the vectors in the DKL space. The R/G and B/Y Gabor patches were identified in the DKL space by vectors aligned along the horizontal axes and the luminance Gabor patches by vectors along the vertical axis.

Contrast sensitivity as a function of spatial frequency is different for B/Y, R/G, and luminance stimuli. Previous results have shown that the R/G and B/Y sensitivities show a low-pass contrast sensitivity function (CSF), whereas luminance sensitivity has a band-pass CSF (Granger & Heurtley, 1973; Humanski & Wilson, 1992; Kelly, 1983; Mullen, 1985). We conducted a preliminary control experiment to determine the optimal spatial frequency sensitivities for the B/Y, R/G, and luminance stimuli. Two of the authors performed a contrast detection experiment (explained in detail in Methods: Experiment 1), for radially and tangentially oriented Gabor patches with close to optimal spatial frequencies as found in the literature (Mullen & Kingdom, 2002) and with twice the optimal spatial frequencies. For R/G and B/Y Gabors the spatial frequencies used were 0.4 and 0.8 c/° and for luminance Gabors 1 and 2 c/°. The detection thresholds were tested on a horizontal meridian position (position A; Figure 1) and an oblique meridian position (position B; Figure 1) at 10° and 15° of eccentricity.

We found that the spatial frequency effect was significant for the chromatic and luminance Gabors ($p < 0.05$). In Figure 2, the contrast thresholds are shown in percentages, with 100% indicating the maximum color contrast that can be achieved on our monitor without producing a luminance artifact. Figure 2A, 2B show the thresholds for the B/Y radial and tangential Gabors for one of the participants. Figure 2C through 2E show the contrast thresholds with respect to eccentricity for the R/G, B/Y, and luminance Gabors respectively. The detection thresholds are lower for chromatic Gabors with 0.4 c/° spatial frequency than for Gabors with 0.8 c/°. The same is true for luminance Gabors with 1 c/° spatial frequency compared to 2 c/°. In Experiments 1 (contrast detection experiment) and 3 (orientation discrimination experiment) we used stimuli with those spatial frequencies observed to be optimal in terms of detection performance: chromatic Gabors with 0.4 c/° and luminance Gabors with 1 c/°. In Experiment 2 (contrast detection experiment) the chromatic and luminance Gabor stimuli had a 1 c/° spatial frequency.

In preparation for Experiments 1 and 3, we determined perceptual isoluminance for the R/G and B/Y Gabors for each participant individually. For this assessment we used the minimum motion technique (Anstis & Cavanagh, 1983). Two Gabors with the same spatial frequency and orientation alternated at a particular location every 0.5 s. The phase of each Gabor was shifted by a quarter cycle to the right compared to the previous one. One Gabor was a luminance one and the other a colored one (either R/G or B/Y). Participants had to adjust the luminance of the colored Gabors until they could not see any consistent motion when the Gabors alternated. We determined isoluminance for the different orientations, spatial frequencies, positions, and eccentricities of the Gabors that were used in the subsequent experiments. We collected five values and selected the median for each condition. In all cases the *elevation* angle of the color Gabors from the isoluminant DKL plane did not vary significantly from zero; thus physical and perceptual isoluminance were similar. For Experiment 3 the stimuli were physically isoluminant to the background.

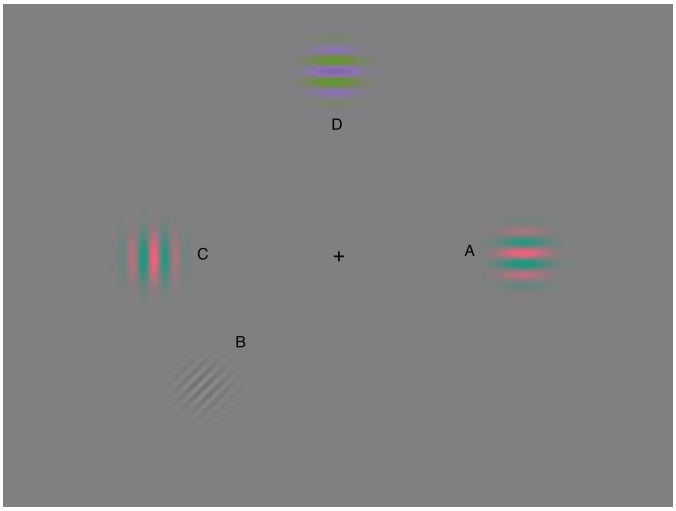

Figure 1. Gabor stimuli at different positions in the visual field. The Gabor stimuli in positions A and B are radially oriented with respect to the fixation point. The Gabors in C and D are tangentially oriented. In the contrast detection experiment (Experiment 1) we tested all four positions. For each position we tested contrast detection thresholds at three eccentricities (10°, 15°, and 18°). In the orientation discrimination experiment we tested positions A, B, and D, and two eccentricities (10° and 15°) for each position.

Apparatus

The experiments took place in two different locations. Experiments 1 and 3 took place in the Institute of Neuroinformatics in the Swiss Federal Institute of Technology (ETH), Zurich; Experiment 2 in the

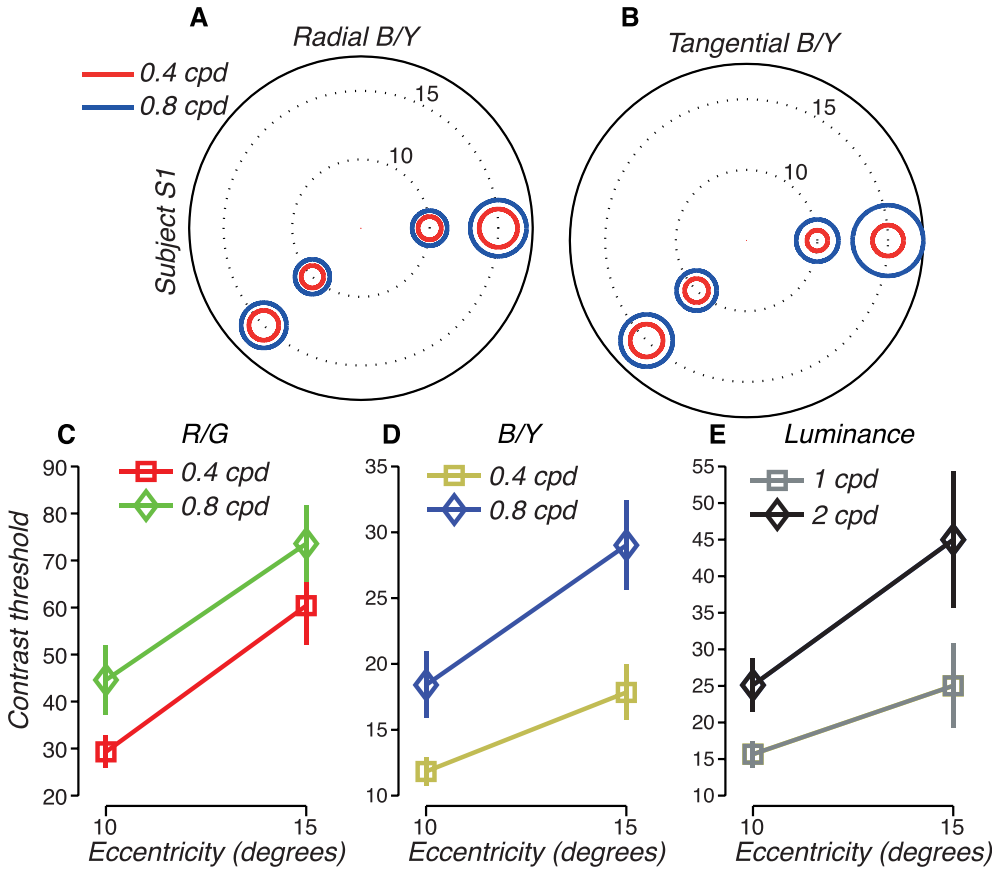

Figure 2. Contrast detection thresholds for different spatial frequencies. (2A, 2B) Contrast detection thresholds for a participant for B/Y Gabor stimuli. The angle indicates the position of the Gabor tested; the magnitude, the distance from the fixation cross (note that the magnitudes are not analogous to the real distances; the closest to the center circles correspond to the contrast detection thresholds of Gabors 10° away from fixation, and the ones right after, thresholds at 15°). The radii of the circles increase linearly with detection thresholds. Figure 2A shows contrast thresholds for radial Gabor patterns, and 2B for tangential Gabors. (2C through 2E) Contrast thresholds for the R/G, B/Y and luminance Gabor patterns as a function of eccentricity for different spatial frequencies. Error bars represent standard error of the mean (*SEM*).

RIKEN Brain Science Institute, Wako, Japan. All the experiments were performed in a darkened room, in which a computer screen was the only light source. Throughout the experiment the participants' heads were maintained in a fixed position with a chin rest positioned 30 cm (50 cm for the contrast detection experiments in Japan) from the screen. Stimuli were presented on a Sony G200P in Zurich and a Sony Trinitron monitor in Japan with a spatial resolution of 800 × 600 pixels and a refresh rate of 100 Hz. The monitors were gamma corrected and were controlled by a Visage graphics board (Cambridge Research Systems). We programmed the experiments in Matlab using the CRS Visage toolbox.

Procedure

Participants were tested over a period of several days, an experimental run lasted approximately 5 min, and participants typically were tested for a half hour to an hour with breaks between each experimental run. Prior to each run, participants freely moved their eyes and located the position of a high contrast stimulus that indicated the position for which they would be tested. Throughout the run, the stimuli appeared only in that position. During the run participants had to always keep their fixation at a small cross positioned at the center of the screen. Auditory signals with distinct pitch and duration at the end of each trial indicated to the participants whether they were correct or not (the one indicating incorrect response was longer and had higher pitch).

Experiment 1

This experiment investigated the contrast sensitivity of tangentially and radially oriented chromatic and luminance Gabor patches with optimal spatial fre-

quencies. In a two-intervals, forced-choice procedure, participants were presented with a grey background with or without a Gabor patch in random order. Participants had to indicate with a button press in which interval they perceived the Gabor. Each interval was preceded by a brief tone that lasted for 500 ms. Intervals were separated by a 500 ms interval during which only the grey background was shown. We varied the contrast of the Gabors according to a staircase protocol. After three consecutive correct responses, the contrast of the Gabor pattern was decreased by a fraction of its contrast; after an incorrect response it was increased by the same amount. The fraction was 0.25 during the first seven staircases; thenceforth it was 0.10. We ran two staircases in each experimental run: one for each of the radially and tangentially oriented Gabors (the stimuli had the same color and were in the same position). Each staircase was completed after twelve reversals. We calculated the contrast thresholds for each Gabor by taking the mean of the last four reversals. The thresholds correspond to a 79% success rate. We tested detection thresholds for three cardinal and one oblique position (shown in Figure 1) and for three different eccentricities (10°, 15°, and 18° from fixation) for each position. A participant had to complete at least nine experimental runs corresponding to the three eccentricities for one position (three eccentricities for each of the B/Y, R/G and luminance stimuli) tested in random order. One participant failed to complete the experiment; another was unable to perceive the Gabors at an 18° eccentricity. Their data were excluded from analysis. Four participants were tested on position A, and three for positions B, C, and D (Figure 1). All five participants were tested in cardinal positions (A, C, and/or D). Three of those participants were also tested in the oblique position (B). Furthermore, three of the five participants were tested in two or more cardinal positions; we averaged the contrast thresholds for the different cardinal positions for each of those participants when setting up our statistical analyses.

The standard deviation of the Gaussian envelope of the wavelet was 0.85°. The envelope was truncated at a radius of 5° from the center. In each trial, the phase of the sinusoidal factor was chosen randomly between 0° and 360° from a uniform distribution. The Gabors were presented in a temporal Gaussian envelope with a standard deviation of 80 ms.

Experiment 2

This experiment investigated contrast detection thresholds for radially and tangentially oriented Gabors with medium spatial frequency (1 c/°). The Gaussian envelope had a standard deviation of 1°. The Gaussian was truncated after 6° from the center of the Gabor. The experimental paradigm was the same as in Experiment 1, except that the stimuli and the interval in-between lasted 160 ms (no temporal Gaussian envelope during stimulus presentation) and the fraction of increase/decrease of the staircase was 0.06 during the first five staircases; thenceforth it was 0.03. The experiment stopped after at least eleven reversals for both patterns. We took the average of the last seven reversal points to estimate thresholds. We tested detection thresholds for eight different positions; in all positions the center of the Gabor was 11° away from fixation. The positions were equally spaced with each other (45° separation) and included the cardinal directions. A participant had to complete at least 24 experimental runs corresponding to the eight positions in the periphery times the type of the stimulus (B/Y, R/G, and luminance) tested in random order.

Experiment 3

This experiment tested the orientation discrimination thresholds of radially and tangentially oriented Gabors at different eccentricities. We measured the orientation discrimination thresholds for R/G, B/Y, and luminance Gabors with the same spatial frequencies as in Experiment 1 (0.4 c/° for color and 1 c/° for luminance stimuli). Stimuli and procedure were the same as in Experiment 1, except the following: a Gabor patch was now present in both intervals of each trial. Participants indicated with a button press whether the orientation of the second Gabor was shifted clockwise or counterclockwise compared to the first one (the reference), which remained the same throughout the experiment. Clockwise or counterclockwise shifts varied randomly with equal probability across trials. The staircase protocol varied the angle difference of the second Gabor compared to the first. The starting difference was 10°. We tested recognition thresholds for three positions (cardinal positions A and D and the oblique position B shown in Figure 1) and for two eccentricities for each position (10° and 15° from fixation) for tangentially and radially oriented reference Gabors. The contrast of the Gabors was at suprathreshold level and was scaled for each participant, orientation, color direction, and eccentricity: always twice the contrast detection threshold found in Experiment 1. Two participants were tested on position A; three, on positions B and D. One of the authors performed the experimental runs for all three positions twice. Another participant performed the experimental runs twice for positions A and B. We took the averages

from these data. Four participants were tested in this experiment. All of them were tested in cardinal positions. Three of them were also tested in oblique positions. One participant was tested in two cardinal positions. We followed the same methodology as in Experiment 1 when setting up our statistical analyses.

Results

Experiment 1: Contrast detection thresholds for radially and tangentially oriented Gabors with optimal spatial frequencies

Figure 3 shows the contrast detection thresholds for radially and tangentially oriented 1 c/° luminance and 0.4 c/° R/G and B/Y Gabors for four positions (three cardinal and one oblique) and three eccentricities (10°, 15°, and 18°). In our analyses in this experiment and Experiment 3 we refrained from making any direct comparisons between the thresholds of any of the color stimuli and the luminance ones, since the color and luminance stimuli that we used here had different spatial frequencies. In Experiment 2, where the color and luminance stimuli had the same spatial frequency, we combined them in a single analysis.

To test whether there is dissociation between R/G and B/Y mechanisms for the cardinal positions, we performed a three-way, repeated-measures ANOVA with color (R/G and B/Y), eccentricity (10°, 15°, and 18°) and orientation (radial and tangential) as repeated factors. We obtained an interaction between color and orientation, $F(1, 4) = 7.8$, $p < 0.05$, indicating that the effects of orientation on contrast thresholds differ between the two colors. We also found an interaction between color and eccentricity, $F(2, 3) = 14.2$, $p < 0.05$, indicating that the contrast sensitivity profile differs between R/G and B/Y Gabors as a function of eccentricity. We then analyzed detection thresholds for the two colored Gabors separately in two-way, repeated-measures ANOVAs with orientation and eccentricity as repeated factors. For R/G Gabors, contrast thresholds were lower for radial orientations compared to tangential ones, $F(1, 4) = 57.9$, $p < 0.01$ (Figure 3A and 3D): a *radial bias* effect. We did not observe this effect for B/Y Gabors, $F(1, 4) = 1.3$, $p > 0.1$ (Figure 3B and 3E). Contrast thresholds increased with eccentricity for R/G Gabors, $F(2, 3) = 14.5$, $p < 0.05$, but not for B/Y ones, $F(2, 3) = 2.9$, $p > 0.1$. In a separate analysis with luminance Gabors we found no effect of orientation, $F(1, 4) = 2.2$, $p > 0.1$, on contrast thresholds. There was a tendency of increasing contrast threshold with eccentricity, $F(2, 3) = 5$, $p = 0.1$.

We then performed an additional analysis for those three participants who were also tested with the oblique

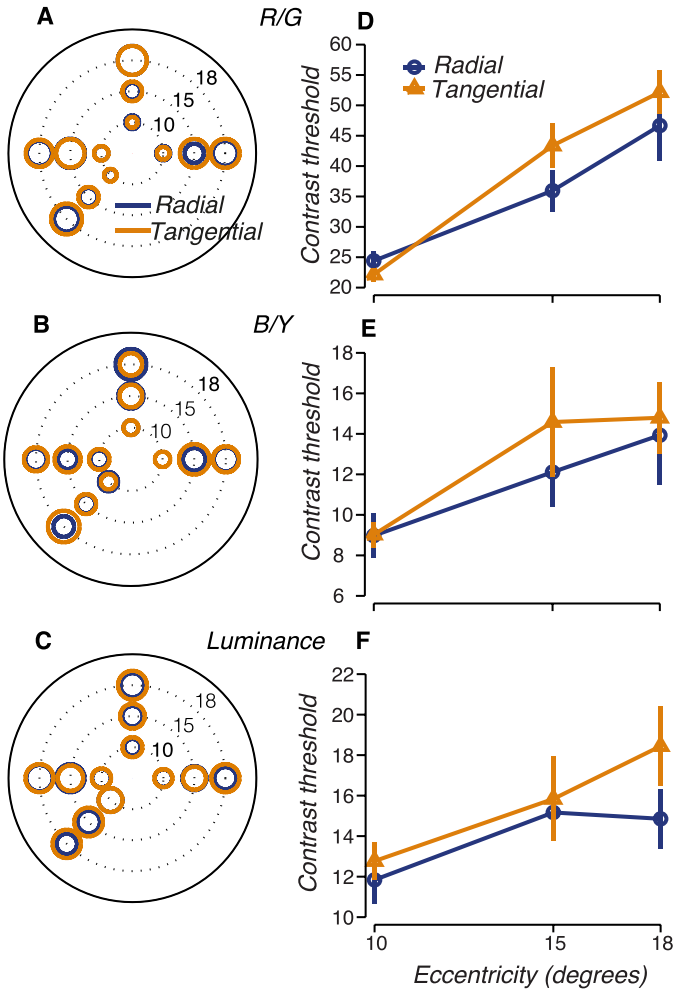

Figure 3. Contrast detection thresholds for radially and tangentially oriented Gabors with optimal—in terms of detection threshold—spatial frequencies (Experiment 1). (3A through 3C) Similarly to Figure 2A, 2B, contrast detection thresholds of radial and tangential Gabors for four positions and three eccentricities (10°, 15°, and 18°) for each position are shown. Each participant's thresholds for a position (3 eccentricities × 2 stimuli orientations = 6 thresholds) have been normalized by his/her highest threshold, so that the maximum value is 1. In each position at least three participants were tested. The radii of the circles represent the mean thresholds. When the thresholds for both tangential and radial Gabors are the same for a location, then only one circle is shown (since both circles completely overlap each other). Figure 3A shows the thresholds for R/G, 3B for B/Y, and 3C for luminance Gabors. (3D through 3F) Contrast detection thresholds for radially and tangentially oriented Gabors as a function of eccentricity. Error bars represent standard error of the mean (*SEM*). Figure 3D shows the thresholds for R/G, 3E for B/Y, and 3F for luminance Gabors.

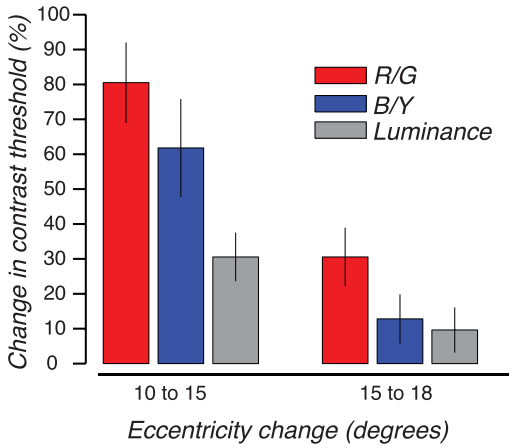

Figure 4. Percent change in contrast detection thresholds from 10° to 15° and from 15° to 18° eccentricity change for both chromatic and luminance Gabors. Error bars represent standard error of the mean (*SEM*).

positions: a four-way, repeated-measures ANOVA with position (cardinal and oblique), color (R/G and B/Y), orientation (radial and tangential), and eccentricity (10°, 15° and 18°) as factors. We found again an interaction between color and orientation, $F(1, 2) = 41.9$, $p < 0.05$. We performed separately for R/G and B/Y stimuli a three-way, repeated-measures ANOVA with position, eccentricity, and orientation as repeated factors. For R/G patterns we observed again a *radial bias* effect, $F(1, 2) = 20.8$, $p < 0.05$, whereas for B/Y ones the difference in contrast thresholds between radial and tangential orientations was not significant, $F(1, 2) = 2.5$, $p > 0.1$. In a separate analysis on the luminance Gabors we found a *radial bias* effect this time, $F(1, 2) = 46.4$, $p < 0.05$; this is in accordance with previous observations in literature (Sasaki et al., 2006). Our results indicate that the difference in contrast sensitivity profiles between tangential and radial stimuli is the same for oblique and cardinal positions since in all our analyses there was no interaction between position and orientation (also no interaction between position and any other factor or no main effect of position), neither for the color nor for the luminance Gabors.

We also analyzed the changes in contrast detection thresholds with eccentricity for the color stimuli. Since there were no main or interaction effects with position, we averaged the contrast thresholds along all the positions (both cardinal and oblique). In a pairwise comparison, we found a difference in the rate of increase of contrast thresholds between R/G and B/Y types $F(1, 4) = 13$, $p < 0.05$. Participants showed a sharper decline in contrast sensitivity (biggest percent change in contrast thresholds) for R/G Gabors compared to the B/Y ones (Figure 4; we also show the percent change for the luminance Gabors).

Experiment 2: Contrast detection thresholds for radially and tangentially oriented Gabors with a 1 c/° spatial frequency

Figure 5 shows the contrast detection thresholds for 1 c/° color and luminance Gabors for eight different positions, each 11° away from fixation. In the analysis for this experiment we also directly compared luminance with color stimuli since all stimuli had the same spatial frequency. We performed a three-way, repeated-measures AVOVA with color direction (R/G, B/Y,

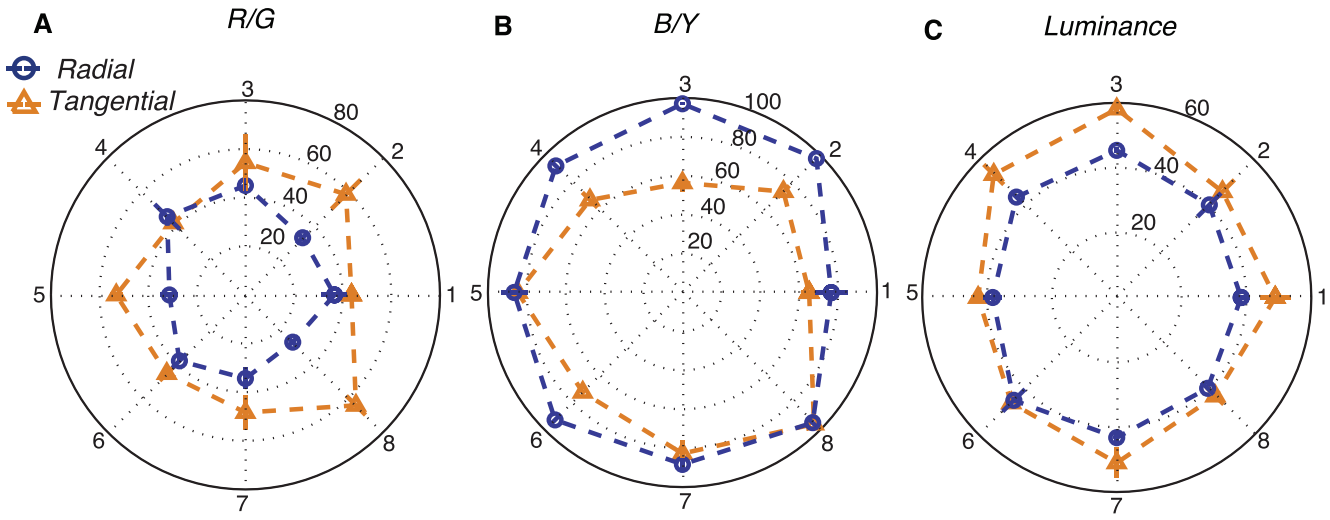

Figure 5. Contrast detection thresholds for radially and tangentially oriented Gabors with 1 c/° spatial frequency for eight different positions 11° away from fixation (Experiment 2). (5A through 5C). The angle of the polar plots indicate the position of the Gabors tested; the magnitude, the contrast thresholds of the Gabors at that position. Error bars represent standard error of the mean (*SEM*).

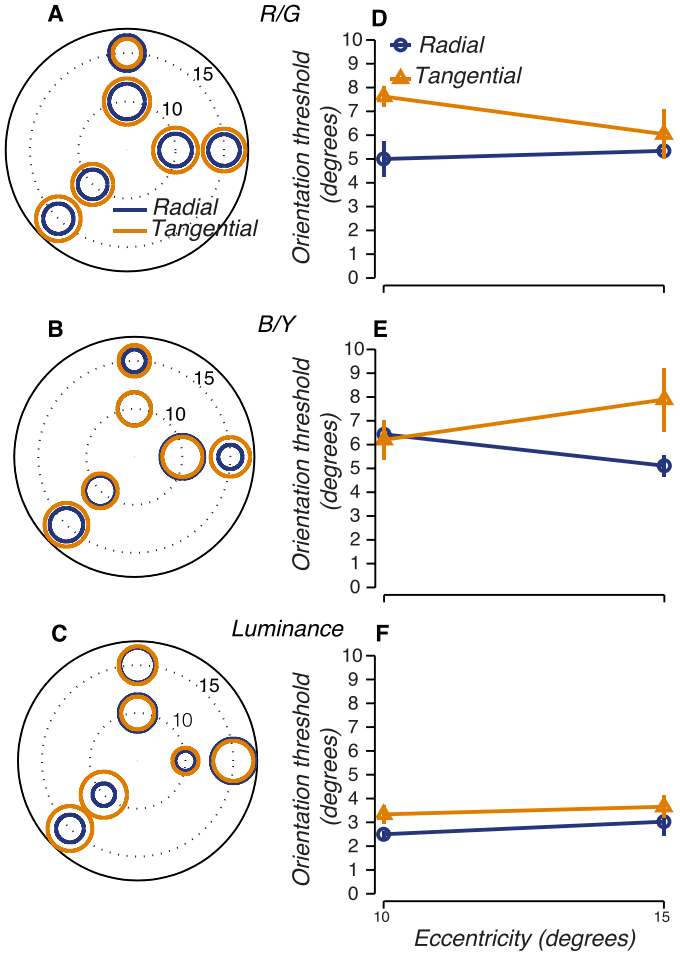

Figure 6. Orientation discrimination thresholds for radially and tangentially oriented reference Gabors with optimal—terms of detection threshold—spatial frequencies and normalized—in terms of multiples of detection thresholds, (taken from Experiment 1)—contrasts (Experiment 3). (6A through 6C) The orientation discrimination thresholds are depicted in a similar way as in Figure 3A through 3C. Three positions (A, B, and D) and two eccentricities (10° and 15°) per position are tested. In positions B and D, three participants were tested; in position A, two participants were tested. (6D through 6F) Similarly to Figure 3D through 3F, orientation discrimination thresholds for radially and tangentially oriented Gabors as a function of eccentricity. Error bars represent standard error of the mean (*SEM*).

and luminance), position (eight positions) and orientation (tangential and radial stimuli) as our factors. Position or any of its interactions with any other factors did not affect contrast thresholds; this result suggests that sensitivity is not affected by overall position. Consistent with the results from Experiment 1, we found an interaction between color direction and orientation, $F(2, 6) = 108$, $p < 0.001$. In separate analysis, we found that participants showed a *radial bias* for R/G, $F(1, 3) = 24.5$, $p < 0.02$ (Figure 5A), and

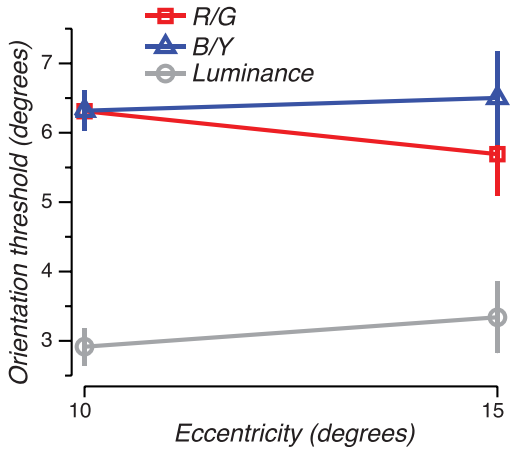

Figure 7. Orientation discrimination thresholds for chromatic and luminance Gabors as a function of eccentricity. Error bars represent standard error of the mean (*SEM*).

luminance, $F(1, 3) = 44.6$, $p < 0.01$ (Figure 5C), patterns. For B/Y patterns participants showed the opposite effect; they were more sensitive to tangential orientations compared to the radial ones, $F(1, 3) = 157$, $p < 0.001$ (Figure 5B). The results in this experiment further solidify the claim that R/G mechanisms show a *radial bias* and B/Y ones do not. They also show that R/G and luminance mechanisms share the same anisotropy.

Experiment 3: Orientation discrimination thresholds for normalized R/G, B/Y and luminance Gabors

Figure 6 shows the orientation discrimination thresholds for radially and tangentially oriented reference 1 c/° luminance and 0.4 c/° R/G and B/Y Gabors with normalized—in terms of multiples (two) of detection thresholds—contrasts for three positions and two (10° and 15°) eccentricities. As in Experiment 1, we first performed a three-way, repeated-measures ANOVA with color, eccentricity, and orientation as factors for the cardinal positions. There were neither main nor interaction effects. In additional separate analyses on color and luminance, we found no difference in orientation discrimination thresholds between tangentially and radially oriented stimuli: $F(1, 3) = 2.77$ for R/G (Figure 6A and 6D), $F(1, 3) = 0.42$ for B/Y (Figure 6B and 6E), $F(1, 3) = 0.14$ for luminance (Figure 6C and 6F), $p > 0.1$.

The same was true for the color stimuli when we included position (oblique and cardinal) as a factor in our analysis for the three subjects that were tested on both cardinal and oblique positions; we found no main or interaction effects. However, for the luminance Gabor we found that the radial orientation thresholds were lower than the tangential ones, $F(1, 2) = 27.7$, $p <$

0.05. Note that the tangentially oriented Gabors typically had greater contrasts than the radially oriented ones, since the contrasts were multiples of detection thresholds (found in Experiment 1) for each color direction, orientation and eccentricity. We did not further investigate if the *radial bias* effect would occur if both tangentially and radially oriented stimuli within the same color direction had the same contrast.

Figure 7 shows the orientation discrimination thresholds for R/G, B/Y, and luminance Gabors (averaged across positions and orientations). There was no difference in thresholds between R/G and B/Y Gabors and no change of thresholds for all stimuli with eccentricity.

Discussion

We observed lower contrast detection thresholds for radially oriented R/G Gabors compared to tangentially oriented ones for both low and medium spatial frequencies. Interestingly enough, when testing for B/Y Gabors we found that participants showed no orientation preference for low spatial frequency stimuli (0.4 c/°), and improved performance for tangential orientations for medium spatial frequency stimuli (1 c/°). Our results from this set of experiments suggest that R/G and luminance channels share a similar anisotropy, but R/G and B/Y channels do not. Overall, our results in the contrast detection experiments suggest that in *nonlocal* orientation processing R/G and luminance channels are functionally similar and both are functionally distinct from the B/Y channel.

In *local* orientation processing, functional segregation between color and luminance channels has already been observed in psychophysical experiments (Mullen, 1985; Mullen & Kingdom, 2002) and in the influential studies by Hubel and Livingstone (1987; Livingstone & Hubel, 1988), providing evidence that both color and form are processed by distinct anatomical regions in V1 and V2. Neuroanatomical and electrophysiological evidence have further suggested that even within the color domain, R/G and B/Y signals are processed by distinct streams, at least early in the visual system, by contrasting retino-geniculo-cortical subsystems. Studies of the retina showed it to have distinct bipolar cells that provide an S-(L-M) cone opponent signal to a specific small bistratified ganglion cell type that drives B/Y vision (Calkins, Tsukamoto, & Sterling, 1998; Dacey, 1996; Dacey & Lee, 1994; Mariani, 1984). Additional physiological studies suggested that this stream remains segregated in the koniocellular layers of lateral geniculate nucleus (Martin, White, Goodchild, Wilder, & Sefton, 1997) and in V1 (Ts'o & Gilbert, 1988).

fMRI studies in humans showed a strong *radial bias* effect for luminance in V1 (Mannion, McDonald, & Clifford, 2010; Sasaki et al., 2006), especially for stimuli presented in the periphery (Freeman, Brouwer, Heeger, & Merriam, 2011). Sumner, Anderson, Sylvester, Haynes, and Rees (2008) also found a small *radial bias* effect for the luminance signal in V1–V3, but not for the R/G and B/Y ones. It is possible that the difference between R/G and B/Y orientation mechanisms is rather subtle and is easily lost within the noise of the BOLD signal.

The mechanisms underlying the *radial bias* effect are not yet clear. One possibility is that the effect in V1 is due to feedforward input from subcortical mechanisms. Levick and Thibos (1982) found that the responses of cat's retinal ganglion cells were biased in favor of sinusoidal drifting gratings that were oriented radially with respect to the fixation point. Leventhal and Schall (1983) suggested that this radial effect could arise because the dendritic fields of retinal ganglion cells are oriented radially, similarly to the spokes of a wheel. Rodieck, Binmoeller, and Dineen (1985) found a similar structure for human ganglion cells with large dendritic fields. Two additional studies showed that cells in the lateral geniculate nucleus (LGN) of the cat (Shou, Ruan, & Zhou, 1986) and monkey (Smith, Chino, Ridder, Kitagawa, & Langston, 1990) responded preferentially to radially oriented stimuli. It is thus possible that the *radial bias* effect is propagated in a feedforward manner from the retina to the LGN and then to the visual cortex.

The *radial bias* effect in V1 may also depend on horizontal connections. These link together neurons with similar receptive field properties, such as orientation preference (Gilbert & Wiesel, 1989; Malach, Amir, Harel, & Grinvald, 1993). Experimental evidence has also shown that horizontal connections link preferentially neurons that not only share the same orientation preference but also have their orientation preference aligned along the same axis (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Schmidt, Goebel, Löwel, & Singer, 1997; Sincich & Blasdel, 2001). A similar anisotropy among horizontal connections for axes along radial orientations could explain the *radial bias* effect. The local-global map hypothesis proposes an organization in V1 in which contextual integration mechanisms induce a *radial bias* (Alexander, Bourke, Sheridan, Konstandatos, & Wright, 2004; Alexander & van Leeuwen, 2010). Nauhaus, Busse, Carandini, and Ringach (2009) showed experimental evidence that lateral connections had a stronger input in V1 compared to feedforward connections when the visual stimulus had low contrast. In the first two of our experiments, where we observed a *radial bias* for R/G but not for B/Y patterns, the contrast of the stimuli was at threshold level.

We examined how contrast detection thresholds vary with eccentricity and found distinct distributions

between the R/G and B/Y Gabors. As in previous studies the contrast detection thresholds' increase with eccentricity was sharper for R/G Gabors compared to the B/Y ones (Mullen & Kingdom, 2002). These results provide additional behavioral evidence that the two color systems are functionally distinct. Previous psychophysical studies showed that R/G visual acuity declines more steeply than the luminance one with eccentricity (Anderson, Mullen, & Hess, 1991; Mullen, 1991), suggesting that R/G color vision is more constrained around the fovea. Furthermore, similarly to our results, Mullen and Kingdom (2002) reported that contrast detection sensitivity for B/Y sinusoidal gratings showed a more gradual decline compared to the one for R/G gratings. The sharp decline of R/G sensitivity with eccentricity suggests that the overrepresented midget bipolar and ganglion cells in the fovea (Dacey, 1993) may play a role in R/G vision. It is likely that the source of this differentiation is not the same from the one that is causing the *radial bias* for the R/G channel but not the B/Y one.

We normalized the contrasts of the Gabors in the orientation discrimination experiment with a common multiple of their contrast detection thresholds. The goal of the normalization process was to equate the signal to noise ratio between the different color directions and orientations at the level of the contrast detection mechanism. That way any effect we see in the orientation discrimination experiment cannot be attributed to differences in contrast detectability between different conditions. Previous psychophysical studies normalized stimuli contrasts with different metrics to compare orientation discrimination thresholds between the luminance and color channels in the fovea (Beaudot & Mullen, 2005; Reisbeck & Gegenfurtner, 1998; Webster et al., 1990; Wuerger & Morgan, 1999). In our experiment we tested orientation discrimination thresholds at different eccentricities. We found that discrimination thresholds of R/G and B/Y stimuli were the same and did not change with eccentricity. In our experiments the different orientations of the stimuli within the same color direction could have different contrasts. It is possible that we would have a different result for a different set of conditions. Thus, we do not claim that there is no *radial bias* or no functional division between R/G and B/Y signals in orientation discrimination. Additional conditions need to be tested for a more conclusive result.

Conclusions

Our results from the contrast detection experiments show a difference in orientation sensitivity between R/G and B/Y signals. Observers showed improved performance for radial patterns compared to tangential ones for R/G signals but not for B/Y ones. These results suggest that there are two distinct *nonlocal* orientation mechanisms in the color system: one that is also selective to R/G patterns and a different one that is selective to B/Y ones. The *radial bias* effect uses contextual information (orientation of the peripheral stimulus with respect to the fixation) that is not constrained within a local region in the visual space. The mechanism responsible for this effect may be different from local processing mechanisms.

In agreement with previous studies, we also found different contrast sensitivity distributions with eccentricity for R/G and B/Y signals. This result also advocates functionally distinct mechanisms. However, since the effect was true both for tangentially and radially oriented patterns, it is possible that the source of functional differentiation in this case is distinct from the one causing the *radial bias*.

Both results advocate functionally distinct R/G and B/Y channels. Functionally distinct color channels do not necessarily imply separate brain regions, each dedicated to a color channel. Still, it is plausible that the separation of function between the color channels unfolds not at the single neuron but rather at a population of neurons that could be common for the different channels (for a review, see Rentzeperis, Nikolaev, Kiper, & van Leeuwen, 2014).

Keywords: radial bias, color, luminance, functional segregation, contrast detection, orientation discrimination, nonlocal processing

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*DCK and CvL are co-senior authors of this article.
Commercial relationships: none
Corresponding author: Ilias Rentzeperis.
Email: ilias@brain.riken.jp.
Address: RIKEN Brain Science Institute, Wako-shi, Japan.

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